

Effects of Environmental Factors on Seed Germination and Seedling Emergence of Common Teasel (*Dipsacus fullonum*)

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Common teasel is an invasive and widespread weed in Argentina. Germination experiments were carried out from 2011 to 2014 to determine the effect of various environmental factors on germination and emergence. Germination of recently dispersed seeds was 12% in darkness at constant temperature. In contrast, seed exposure to light and alternating temperatures enhanced germination to 95%. The requirement of light and alternating temperatures suggest that common teasel has physiological dormancy. Several experiments were carried out to determine whether (1) seed responses to light and alternating temperatures have a hormonal basis, (2) seed coats can suppress germination, and (3) time and thermal conditions during seed storage reduce light and alternating temperature requirements. Germination was reduced ($\leq 13\%$) by a gibberellin synthesis inhibitor. In contrast, the presence of gibberellins and an abscisic acid synthesis inhibitor increased germination to 95 and 38%, respectively. Results suggest that a higher ratio among gibberellins and abscisic acid (GA/ABA) leads to a break in dormancy. Germination was 100% when embryos were excised, suggesting that seed coats may suppress germination by mechanical restriction. Likewise, germination was enhanced by hydrogen peroxide (70%). This compound is known to increase GA/ABA ratio in agreement with a hormonal control of dormancy proposed for common teasel. An increment of storage time reduces light and alternating temperature requirements, allowing seeds to germinate in darkness. Taking these results together confirms that common teasel has physiological dormancy. Seedling emergence was progressively reduced from 70 to 8% by increased burial depth from 0 to 3 cm. Information from these experiments may facilitate development of effective management for common teasel.

Nomenclature: Common teasel *Dipsacus fullonum* L. DIFU2.

Key words: Alternating temperatures, depth of burial, GA/ABA ratio, physiological dormancy, germination, light.

Common teasel is a very aggressive, biennial, exotic species capable of colonizing natural and improved pastures, abandoned fields, and roadsides. Common teasel plants are herbaceous and 0.5 to 2 m tall and have prickles on stem and leaves. Rosettes have large leaves that cover the soil around them, reducing resources available for establishment of other species (Rector et al. 2006). Reproduction and dispersion is exclusively through seeds, and each plant produces around 3,000 seeds per year (Werner 1975). Because of this trait, knowledge of seed

biology of this species is essential for developing sustainable management practices (Bhowmick 1997; Chauhan and Johnson 2008). Common teasel was observed in more than 40 U.S. states and four Canadian provinces (Rector et al. 2006; USDA 2015; Werner and Caswell 1977). In Argentina, even though it was detected decades ago, colonized area has increased significantly in the past years, and it is considered one of the most abundant weed species in grasslands and right of ways (Busso et al. 2013; Marzocca 1976). Nevertheless, no information is available related to seed germination and seedling establishment of Argentinian seed populations.

Germination and emergence are important processes for weed establishment and persistence. Environmental factors, such as temperature and light, modulate these processes and influence weed presence in the field. Werner (1975) and Beaton and Dudley (2007) reported that total germination of common teasel seeds exposed to light, alternating temperatures, or both reached values $> 90\%$. In contrast, no information exists regarding their

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germination under other environmental conditions, such as darkness. Batlla and Benech-Arnold (2010) pointed out that the stimulus of alternating temperatures, light, or both are essential for germination of many species that have physiological dormancy (Finch-Savage and Footitt 2012). Requirement of one or both stimuli are gradually reduced as seeds lose their dormancy under natural or artificial conditions (e.g., cold stratification or dry after-ripening); in many cases, when dormancy level is sufficiently low, seeds are able to germinate, even at constant temperature in darkness (Benech-Arnold et al. 2000). To date, germination requirements of Argentinian common teasel seeds are not known, and some key questions are: (1) Is there a specific requirement of alternating temperature, light, or both to germinate? (2) Are any of these stimuli, when present alone, enough for common teasel to germinate? (3) Are common teasel seeds dormant at the time of dispersion?

Physiological dormancy is the most abundant form of dormancy in temperate species and is found in seeds of gymnosperms and all major angiosperm clades (Finch-Savage and Leubner-Metzger 2006). Some features of this type of dormancy include: embryos excised from seeds producing normal seedlings; dormancy broken by gibberellin (GA) treatment and, depending on the species, by scarification; after-ripening in dry storage; and cold stratification. Responses of common teasel seeds to these treatments will provide precise information about the existence and type of dormancy present in this species. As expressed above, light and alternating temperatures act as environmental stimuli to terminate dormancy. Once perceived by seeds, they regulate the expression of genes involved in hormone synthesis and degradation and regulate the ratio between abscisic acid (ABA) and GA content (Footitt et al. 2011). Both ABA and GAs are considered key hormones in the induction of seed dormancy and promotion of seed germination, respectively (Linkies and Leubner-Metzger 2012). In particular, the ratio of content between these two hormones are important in regulating induction, maintenance, and termination of dormancy (Finkelstein et al. 2008). The termination of dormancy requires low ABA/GA ratios. In contrast, the maintenance of dormancy is associated with high ABA/GA ratios (Finch-Savage and Leubner-Metzger 2006). The involvement of these hormones in light or alternating temperature responses has not been studied for common teasel.

The general aim of our research was to obtain a better understanding of seed germination and emergence responses of common teasel to different factors and environmental conditions. The particular objectives of this study were to (1) evaluate light and alternating temperature requirements on germination, (2) determine whether seed responses to light and alternating temperatures are hormonally regulated, (3) determine whether common teasel has physiological dormancy, and (4) evaluate the influence of depth of burial on emergence.

Materials and Methods

Seed Source and Preparation. Common teasel seeds were collected in January 2011 and 2012 at the School of Agriculture, Catholic University of Argentina (UCA) campus (34.57°S; 58.28°W). Seed heads were collected from many randomly selected plants, and seeds were manually separated from each head and bulked. Seeds were then surface-sterilized by immersion in a 0.5% sodium hypochlorite solution for 10 min, then rinsed with distilled water several times and dried at room temperature. After that, dry seeds were kept at 6 C until the beginning of experiments.

General Procedure for Germination Studies. All experiments were conducted from 2011 to 2014 at the Seed Laboratory (School of Agriculture, UCA, Buenos Aires City, Argentina). All experiments were performed twice and consisted of four replicates of 30 sterilized seeds of common teasel. Seeds were placed on 9-cm petri dishes lined with two sheets of filter paper (Double Ring #102 Hangzhou Special Paper Industry Co. Ltd., China) in all experiments, unless stated otherwise. Filter papers were moistened with 8 ml of distilled water or corresponding test solution. All petri dishes were placed in plastic bags (Ziploc®, Johnson & Johnson, New Brunswick, NJ) to prevent dehydration and were kept for 21 d in germination chambers with 20/10 C day/night temperatures and 15 C for alternating and constant temperature treatments, respectively. Temperatures used represent typical fall average high and low temperatures in our region. Light treatment was accomplished by seed exposure to six fluorescent Philips 40/15 40W lamps (Philips, Eindhoven, The Netherlands) to obtain a calculated proportion of phytochrome (Pfr form) of 0.87 (Casal et al. 1991), whereas dark treatment involved covering petri dishes with two layers of aluminum foil. Germinated seeds for light treatments were counted daily

until day 21, whereas germination for dark treatment was determined at day 21. Seeds with visible radicle protrusion were considered germinated and were removed.

Effects of Alternating Temperatures, Light, Trinexapac-Ethyl, and Gibberellins on Seed Dormancy Breakage. To evaluate seed requirement of alternating temperatures, light, or both for germination and the participation of GAs on breaking dormancy, common teasel seeds were incubated at a combination of three factors: temperature (two levels), light (two levels), and media (two kinds). Temperature treatments were alternating (20/10 C, 12 h each) and constant (15 C). Light treatments were 12/12 h light/dark (light) and 0 h light (darkness). Media treatments were distilled water (H₂O) and 250 µM trinexapac-ethyl (TE). Trinexapac-ethyl is a GA synthesis inhibitor (Rademacher 2000; Yamaguchi et al. 2008). Data was analyzed using a factorial design with three factors.

Effect of GAs and Fluridone on Dormancy Breakage. Seeds were incubated in darkness at constant temperature (15 C). Gibberellin treatments were: 0, 50, and 250 µM GA₃ (Sigma Chemical Company, St. Louis, MO). The positive control was 15 C + light + 0 µM GA₃. To determine whether primary dormancy is related to ABA present in the seed, seeds were incubated in darkness at 15 C in 10, 50, and 100 µM fluridone (PhytoTechnology Laboratories, Shawnee Mission, KS). Fluridone is an ABA synthesis inhibitor (Yoshioka et al. 1998). Additionally, seeds were incubated in a mixed solution of 50 µM fluridone + 250 µM GA₃. The pH of each solution was corrected to 6.5.

Effect of Seed Coat on Seed Germination. To determine whether seed coat restricts seed germination, a surgical excision of embryos was carried out. Seed coats were cut at the end opposite the embryo with a scalpel, aided by tweezers and a magnification glass. Four replicates of 25 intact embryos were located in 9-cm petri dishes on two filter paper discs moistened with 8 ml of distilled water. Dishes were incubated for 9 d at 15 C in darkness, and then germination was scored. Excised embryo germination was compared with that of whole seeds incubated for 21 d at 15 C in light (positive control) and in darkness (negative control).

Effect of Nitrogenous and Oxidant Treatments on Seed Germination. Four treatments, one rate of 0.2%

potassium nitrate (KNO₃) and three rates of hydrogen peroxide (0.9, 4.5, and 8.9 M), were tested on common teasel germination. All treatments were performed using 30 seeds per petri dish and four replicates. Seeds were incubated at 15 C in darkness for 21 d. A positive control (15 C and light for untreated seeds) and a negative control (15 C and darkness for untreated seed) were also included.

Effect of Chemical and Mechanical Scarification on Seed Germination. Chemical scarification treatment was performed by seed imbibition in concentrated sulfuric acid (H₂SO₄) at 0, 5, 15, 45, or 90 min. Seeds were washed with tap water and dried on absorbent paper. Mechanical scarification treatments consisted of (1) sanding the end opposite the embryo five times with sandpaper (no. 200) and (2) sanding the entire seed surface five times longitudinally on both sides. Sanded seeds were used to perform a germination test at 15 C in darkness.

Effect of Time and Temperature Storage on Seed Dormancy Relief. To determine the effect of time and temperature on a reduction of light or alternating temperatures as a requirement for germination, recently dispersed seeds were exposed to a combination of two treatments, cold stratification (i.e., hydrated seeds at 6 C) and dry after-ripening (seeds dried at 15 C), and four durations, 0, 4, 8, and 12 wk. After completion of the stratification treatments, seeds were incubated at 15 C in darkness for 21 d, when germination was recorded.

Effect of Seed Burial Depth on Seedling Emergence. The effect of seed burial depth on seedling emergence was studied in germination chambers set at 20/10 C (12/12 h light/dark). Eight seeds were placed on soil surfaces of 10-cm-diam plastic pots and covered with soil to 0, 0.5, 1, 1.5, 2, and 3 cm depth (five replicates per sowing depth). Soil used was sterilized topsoil and perlite mixed at 2 : 1 (v/v). Containers were watered as needed to maintain optimum soil moisture for seed germination. Seedlings were considered emerged when cotyledons were visible. Seedling emergence was recorded 14 d after sowing.

Statistical Analysis. Data were subjected to ANOVA using a completely randomized design with four replicates for all experiments unless otherwise stated. Data presented are averages across two experimental runs because there was no significant experiment by treatment interaction.

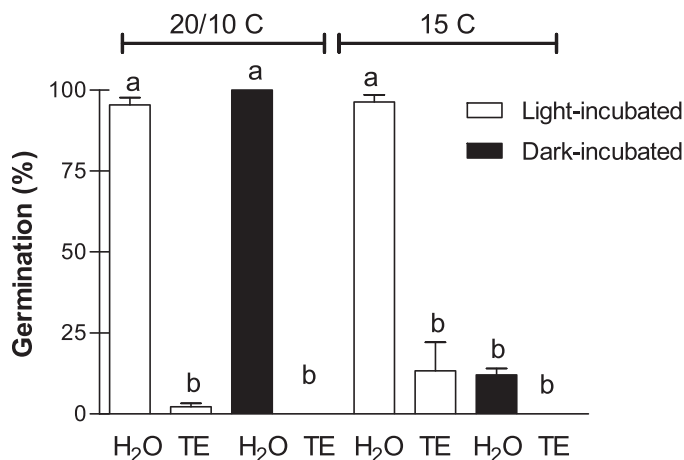


Figure 1. Effect of temperature, light, and incubation medium on germination of common teasel seeds. TE is a gibberellin synthesis inhibitor (see Materials and Methods). T bars indicate the standard error. Different letters at the tops of the bars indicate significant differences according Tukey's test ($P < 0.05$).

Means were separated using Tukey's test at $P < 0.05$. Data were analyzed using Infostat (Di Rienzo et al. 2013).

Results and Discussion

Effects of Alternating Temperatures, Light, and GAs on Germination. There was a three-way interaction between temperature, light, and incubation media ($P < 0.001$). Within H₂O treatments, a combination of alternating temperature (20/10 C) in light ($96 \pm 2\%$) (mean \pm SE) and in darkness (100%), and constant temperature (15 C) in light ($96 \pm 2\%$), showed the highest germination, with no differences between them (Figure 1). The lowest germination in H₂O was for constant temperature (15 C) in darkness ($13 \pm 8\%$). Addition of TE to media reduced germination of all treatment combinations with either alternating temperature and light or both, which had the same low germination that scored at constant temperature in darkness (Figure 1). Also, low germination in all TE treatments was similar to that obtained in H₂O at constant temperature and darkness (Figure 1). These results suggest that common teasel seeds are dormant at the time of dispersion, but it does not require both alternating temperatures and light to germinate. Either alternating temperatures or light are enough to trigger germination of common teasel. Total germination obtained in this study was in agreement with Werner (1975). Reduction in germination by TE suggests that GAs have a role in breaking seed dormancy. Alternating temperatures

or light requirement for germination of this population agrees with field conditions for common teasel germination in our region. Werner (1975) reported that common teasel germination is favored by open gaps, where temperature fluctuations are wide and the incoming light, with a high red to far red ratio, satisfies both germination requirements. Therefore, those agronomic practices, such as seed burial or the presence of closed canopies, which prevent seeds from receiving these signals, would reduce germination of recently dispersed seeds. Additionally, common teasel seed viability is short, not exceeding 2 yr (Werner and Caswell 1977). Consequently, use of these practices together with prevention of a new seed rain would progressively reduce seed bank size.

Effect of Gibberellins and Fluridone on Seed Germination. Several authors reported that termination of dormancy by alternating temperature and light is related to an increase in GA/ABA ratio (Huarte et al. 2014; Sawada et al. 2008; Toyomasu et al. 1998). Low germination obtained in TE, which was similar to that scored at constant temperatures in darkness, suggested that breaking of dormancy is mediated by GAs. We wanted to evaluate whether the addition of exogenous GAs and the inhibition of ABA synthesis, by means of fluridone, increase germination. Although 50 μ M GAs at constant temperature in darkness did not increase germination, 250 μ M GAs increased germination to percentages similar to those of alternating temperatures and light positive control (Figure 2A). The presence of fluridone at constant temperatures (15 C) in darkness enhances germination in relation to negative control (i.e., 15 C + dark; $P < 0.001$) (Figure 2B). The three fluridone concentrations tested were equally effective to increase germination (38 ± 8 , 36 ± 10 , and $25 \pm 6\%$ for 10, 50, and 100 μ M, respectively) when compared with negative control (i.e., 15 C + dark). However, germination was still 50% lower than the positive control (15 C + light) which had the greatest germination ($75 \pm 4\%$). Increment of GA/ABA ratio, by means of exogenous GAs or blocking ABA synthesis, increases seed germination. Taken together, these results could suggest that breaking of common teasel dormancy is under hormonal regulation. These results agree with those reported for other species with physiological dormancy, where a higher GA/ABA ratio triggers germination. A high GA/ABA ratio promotes synthesis of cell wall remodeling proteins, which are responsible for increasing embryo growth potential, seed coat

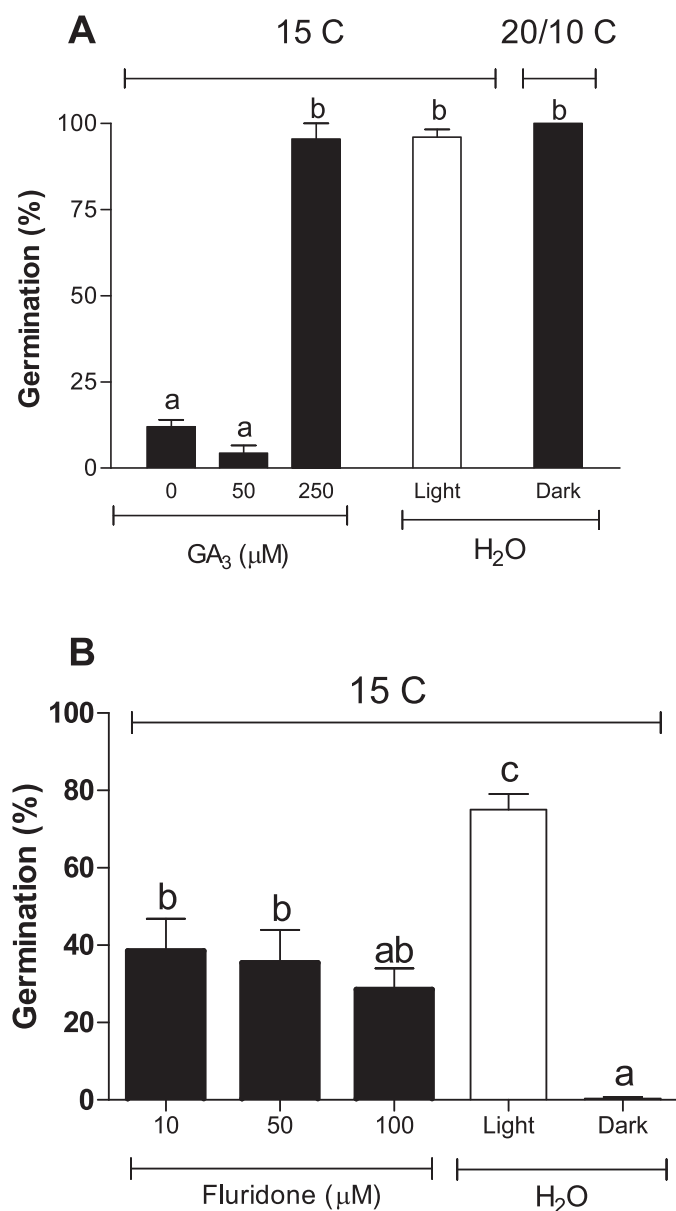


Figure 2. (A) Germination of common teasel seeds exposed to constant 15 C + dark + different GA₃ concentrations (black columns), fluctuating temperatures (20/10 C) + dark + H₂O (black column), and constant 15 C + light + H₂O (white column). (B) Germination of common teasel seeds exposed to constant 15 C + dark + different fluridone concentrations (black columns), and constant 15 C + light + H₂O (white column). T bars indicate the standard error. Different letters at the top of each bar indicate significant differences according Tukey's Test $P < 0.05$).

weakening, or both, leading to germination (Linkies and Leubner-Metzger 2012).

Effect of Seed Coat on Germination. Germination of excised embryos incubated at 15 C in darkness was 100%, which is no different from that scored in the positive control (15 C + light) (Figure 3). These results, together with the enhancement of germina-

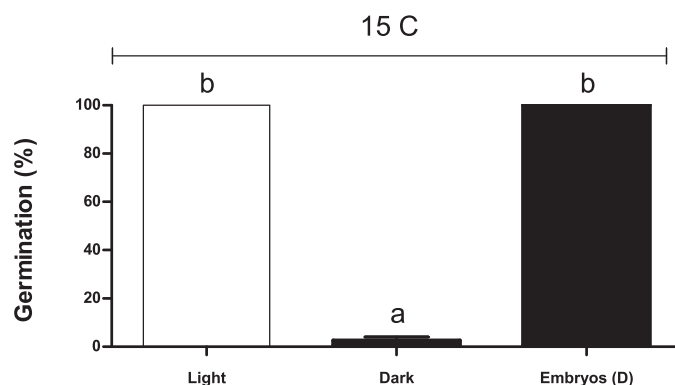


Figure 3. Germination of common teasel seeds and isolated embryos exposed to 15 C + dark (black columns) and constant 15 C + light (white column).

tion by means of GAs (Figure 2A), suggest that physiological dormancy is the type of dormancy present in common teasel. Based on the hormonal response, germination impairment by seed coats seems to be mechanical. However, seed coats can also impede germination by other mechanisms (Nasreen et al. 2002). To solve this issue, we conducted additional experiments.

Effect of Scarification on Seed Germination.

Sulfuric acid-treated seeds for 5 min and subsequent incubation in water at 15 C in darkness obtained greater germination ($18 \pm 1\%$) than that of the negative control ($0.4 \pm 0.4\%$) and all other H₂SO₄ treatments (15, 45, and 90 min). However, efficiency of this treatment to enhance germination was not enough to get closer to the positive control (15 C + light; $P < 0.0001$) (Figure 4A). Increase in germination by H₂SO₄ treatment was less than that reported for other species (e.g., Aliero 2004; Aref et al. 2011; Muhammad and Amusa 2003), where the effect of H₂SO₄ scarification was suggested to be based on an increased seed permeability to water. Therefore, a reduced water uptake does not seem to be the cause of germination inhibition by seed coats. Absence of germination observed in H₂SO₄ exposures longer than 5 min could be due to lesions in embryo vital parts (Aliero 2004). Mechanical scarification by sanding one end or both sides of the seed only increased slightly the germination of seeds incubated at 15 C in darkness compared with the untreated seed of the negative control (15 C + darkness; $P < 0.0001$) (Figures 4B and 4C). Germination for seeds sanded on one end or both sides was 14 ± 6 and $9 \pm 2\%$, respectively. Taking these results together, it seems that seed coats do not inhibit seed germination by limiting water uptake and or gaseous exchange.

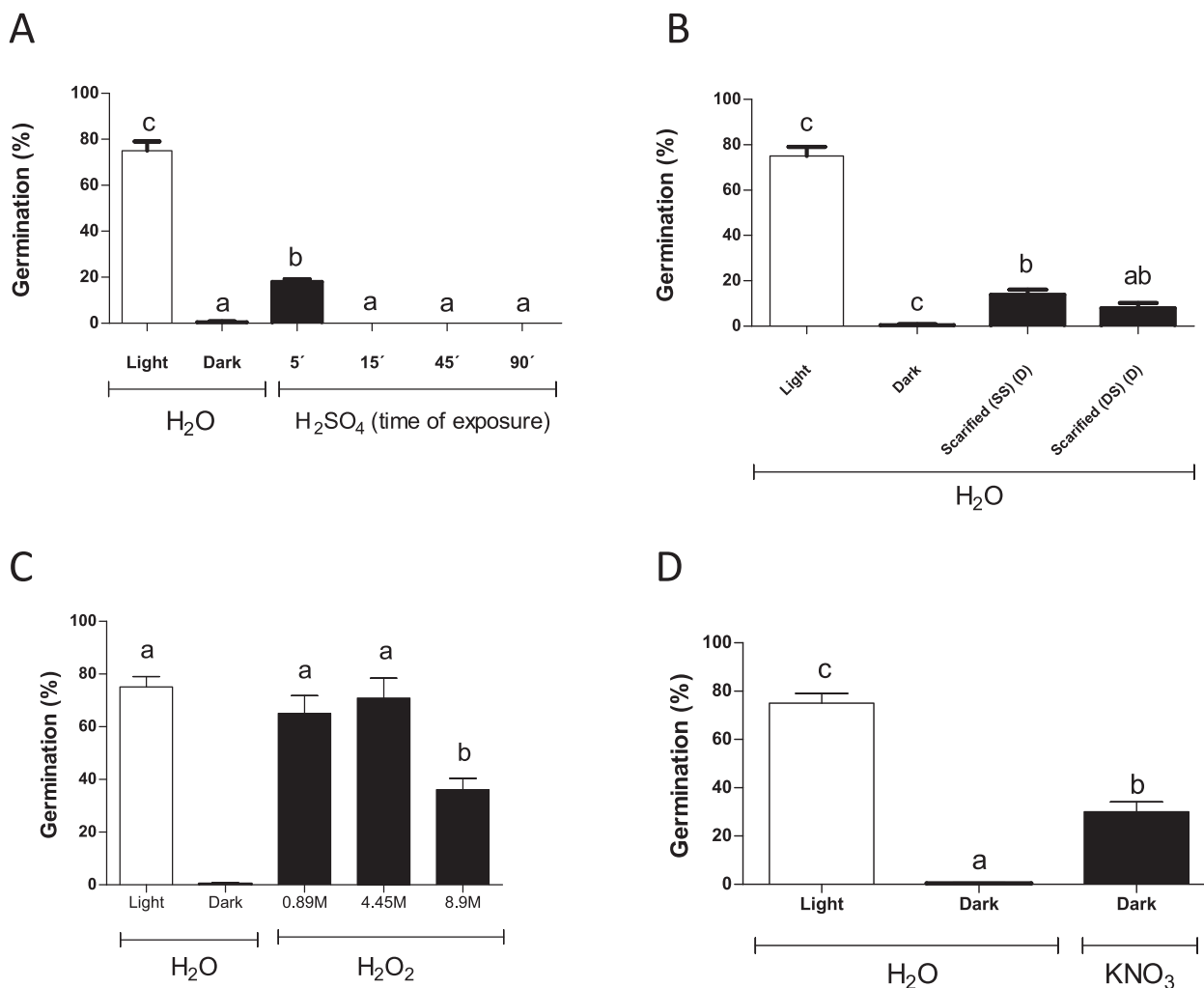


Figure 4. (A) Germination of common teasel seeds exposed to constant 15 C + dark + different H₂SO₄ exposure times (black columns), constant 15 C + dark + H₂O (black column), and constant 15 C + light + H₂O (white column). (B) Germination of single- and double-side scarified common teasel seeds exposed to constant 15 C + dark + H₂O (black columns), constant 15 C + dark + H₂O (black column), and constant 15 C + light + H₂O (white column). (C) Germination of common teasel seeds exposed to constant 15 C + dark + H₂O (black columns), constant 15 C + dark + H₂O (black column), and constant 15 C + light + H₂O (white column). (D) Germination of common teasel seeds exposed to constant 15 C + dark + KNO₃ (black columns), constant 15 C + dark + H₂O (black column), and constant 15 C + light + H₂O (white column). T bars indicate the standard error. Different letters at the top of each bar indicate significant differences according Tukey's Test ($P < 0.05$).

Effect of Nitrogenous and Oxidizing Compounds on Seed Germination. Incubation in KNO₃ at 15 C in darkness increased germination to values intermediate to those scored in both controls ($P < 0.0001$) (Figure 4D). Germination in KNO₃ reached $30 \pm 4\%$, whereas negative and positive controls scored 0.4 ± 0.4 and $75 \pm 4\%$, respectively. Likewise, germination obtained in 0.89 and 4.45 M H₂O₂ was $65 \pm 7\%$ and $70 \pm 8\%$, respectively, and did not differ from the positive control (15 C + light; $P < 0.0001$) (Figure 4E). The positive effect of H₂O₂ on seed germination has already been reported for many species (Schmidt 2000). Different mechanisms were pro-

posed for this response. Liu et al. (2010) indicated that presence of H₂O₂, both endogenous and exogenous, increased ABA catabolism and GA biosynthesis. This role is consistent with our results, in which the addition of GAs and a reduction of ABA synthesis were effective in promoting common teasel germination.

Effect of Seed Storage on Dormancy Relief. Germination of seeds treated with cold stratification was 43 to 58%, contrasting with no germination when seeds were not stratified ($P < 0.001$) (Figure 5A). In contrast, stratified seeds at 4 and 8 wk reached 43 ± 11 and $58 \pm 3\%$, respectively. Extension of the stratification period to 12 wk lead

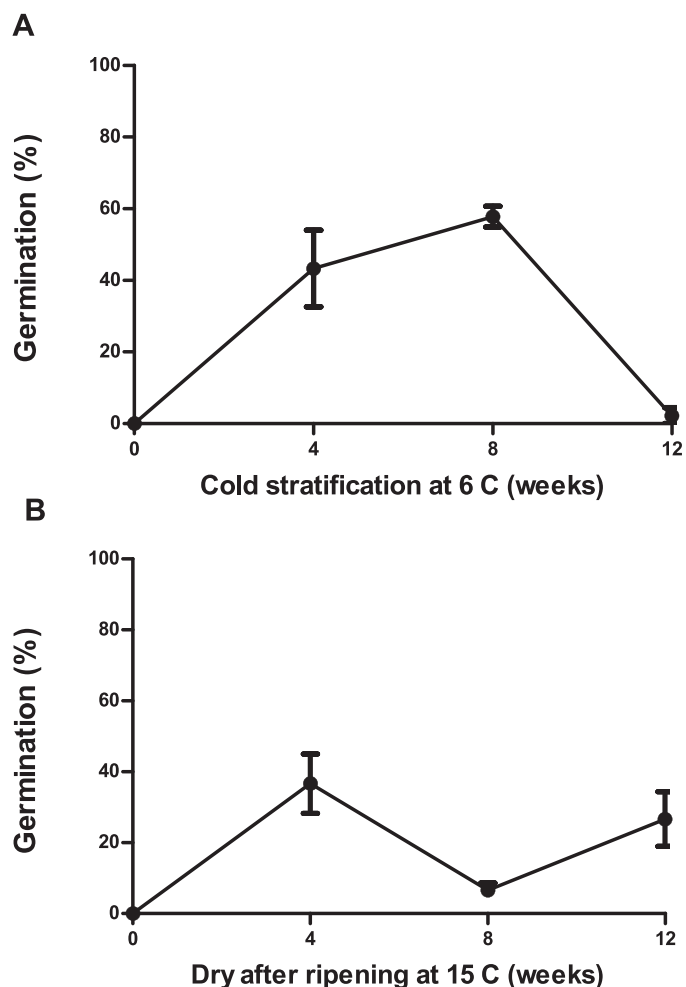


Figure 5. (A) Germination of common teasel seeds exposed to different cold stratification weeks durations + constant 15 C + dark + H₂O (B). Germination of common teasel seeds exposed to different dry after-ripening weeks durations + constant 15 C + dark + H₂O. T bars indicate the standard error.

to a sharp reduction in germination ($2 \pm 2\%$), probably because of induction into secondary dormancy. Our results suggest that recently dispersed seeds would be unable to germinate in the absence of light, and/or alternating temperatures. Therefore, buried seeds would only partially be able to germinate at the end of winter or early spring after dispersion. Seed storage at 15 C increased germination from 0 to 37 ± 8 , 7 ± 2 , and $33 \pm 7\%$ for 0, 4, 8, and 12 wk of storage, respectively (Figure 5B). These results partially agree with those of Bentivegna (2008), who reported an increase in seed germination with greater period of storage.

Effect of Seed Burial Depth on Seedling Emergence. Seed burial depth greatly affected seedling emergence of common teasel ($P < 0.0001$) (Figure 6). Seedling emergence was greatest when seeds were placed on the soil surface

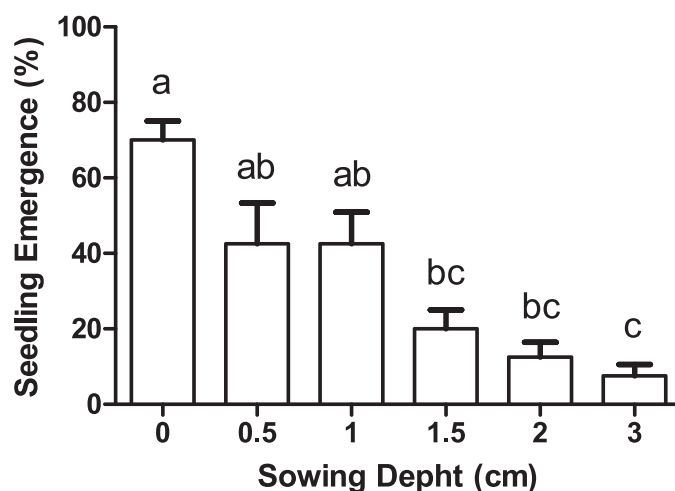


Figure 6. Depth of emergence of common teasel seedlings. Data points are the means. T bars indicate the standard error.

or buried shallowly ($70 \pm 5\%$, 42 ± 11 , $42 \pm 8\%$ for 0, 0.5, and 1 cm depth). In contrast, seedling emergence at deeper depths decreased to 20 ± 5 , 12 ± 4 , and $7 \pm 3\%$ for 1.5, 2, and 3 cm, respectively. Decreased seedling emergence because of increased burial depth has been reported for several weed species (Benvenuti et al. 2001; Boyd and Van Acker 2009). Small-seeded species might have not enough energy reserves to support elongation from deeper depths. Also, a reduction in the amount of light with increasing burial depth has been suggested to reduce weed emergence from greater depths (Benech-Arnold et al. 2013). Results suggest that tillage operations leading to seed burial beyond maximum depth of emergence (i.e., 3 cm) would minimize seedling emergence.

Results of this study indicate that Argentinean common teasel populations experience physiological dormancy. Light, fluctuating temperatures, or both were effective in breaking seed dormancy. The presence of TE reduced germination, suggesting that GAs have a role in breaking dormancy in common teasel. Likewise, exogenous GAs and fluridone in dark constant temperature-treated seeds increased germination, proposing that dormancy is under hormonal control. Dry after-ripening and cold stratification were effective in releasing seeds from this state. Excision of embryos from seeds induces full germination at constant temperature in darkness. This result, together with the increased germination after addition of GAs, confirms that the type of dormancy in common teasel is physiological. This result was supported by the effect of H₂O₂ on germination. The physiological effect of this compound was related to an

increase of ABA catabolism and GA biosynthesis, consistent with the observed effect of GA addition and ABA reduction on common teasel germination.

The results presented here propose that, as for other weed species that require light or fluctuating temperatures to germinate, defoliation patterns selected for pasture management would prevent the fulfillment of both germination requirements by common teasel seeds (e.g., by maintaining some residual leaf area after mowing to reduce both the thermal fluctuations and the light reaching the soil surface). Once common teasel seeds loses its dormancy, and consequently its germination requirements, the presence of a closed canopy will reduce the possibility of common teasel seedling establishment because of its small seedling size. Also, seedling emergence was optimal at shallow burial depths, indicating that farming practices that bury seeds beyond the maximum zone of emergence would minimize seedling emergence. Inferences from obtained results should therefore be tested in field experiments.

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